

AGGRESSIVE RESPONSE OF CHICKADEES TOWARDS BLACK-CAPPED AND CAROLINA CHICKADEE CALLS IN CENTRAL ILLINOIS

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ABSTRACT.—Aggressive responses of Black-capped (*Poecile atricapillus*) and Carolina chickadees (*Poecile carolinensis*) to heterospecific and conspecific vocalization playbacks were measured across a historic contact zone in east-central Illinois to determine the magnitude of interspecific aggression. Within the traditional Carolina Chickadee range, chickadees responded more aggressively towards Carolina Chickadee calls than Black-capped Chickadee calls. Within the traditional Black-capped Chickadee range, chickadees did not respond to either vocalization significantly more than the other. The aggressive response towards presumed heterospecific vocalizations for all chickadees was marginally more aggressive closer to the contact zone. Thus, we conclude that interspecific aggression may not act as a gap producing mechanism between chickadee ranges. Received 24 Nov. 1998, accepted 31 March 1999.

Black-capped (*Poecile atricapillus*) and Carolina (*Poecile carolinensis*) chickadees are extremely similar in appearance, behavior, and ecology (Brewer 1963, Johnston 1971, Merritt 1978). They occupy largely parapatric breeding ranges, although there are a few narrow zones of overlap. Interspecific encounters and recognition of heterospecifics are common in these overlap areas (Ward and Ward 1974). Interspecific territoriality in chickadees is rare except with other chickadees in contact zones (Brewer 1963, Smith 1993). Interspecific territoriality may arise through the competition for limited resources, which may contribute to a competitively-induced gap between Black-capped and Carolina chickadee ranges (Tanner 1952, Slade and Robertson 1977).

We measured the level of aggression exhibited by chickadees across a historic contact zone in Illinois defined by Brewer (1963) to test the role of interspecific aggression as a range segregating mechanism. We hypothesized that responses towards the conspecific vocalization would be more aggressive than those to heterospecific vocalizations. We also hypothesized that levels of aggression to heterospecific vocalizations would be greatest closer to the contact zone and weaker away from the contact zone. We expected this re-

sponse because closer to the zone of overlap chickadees would have more encounters with congeners and therefore should exhibit more aggressive territorial defense if interspecific aggression is used to maintain range boundaries.

METHODS

Study area.—Our 5 study sites formed a transect across the historical contact zone for chickadees in east-central Illinois (Fig. 1). The distance from the midline of the contact zone varied for each study site (Shelbyville 10 km, Douglas Hart 22 km, Fox Ridge 40 km, Lincoln Trail 58 km, Sangchris 65 km). Sangchris State Park and Shelbyville State Park were located in traditional Black-capped Chickadee range. Fox Ridge State Park, Douglas Hart Nature Center, and Lincoln Trail State Park were located in traditional Carolina Chickadee range. Study sites were visited weekly.

Playback experiments.—Two chickadee calls and one White-breasted Nuthatch (*Sitta carolinensis*) vocalization were used in this experiment. A playback tape (Maxell UD11 60 minutes) was made for each vocalization on a Magnavox FA9403 dual recording stereo system. Each tape had a call rate of 18 calls/minute. Vocalizations of both chickadee species and the White-breasted Nuthatches were taken from the Peterson Guide to Bird Songs® (Peterson 1983). One call of each species was used for all trials. This seemed reasonable given that differences between species calls are much greater than variation of calls within a species. Vocalizations were played to subjects on a Panasonic FW18 dual speaker cassette recorder.

Playbacks were used to test the abilities of chickadees to discriminate between conspecific and heterospecific vocalizations (Emlen et al. 1975). Several researchers have shown that chickadees respond to conspecific songs more than to heterospecific songs (Hill and Lein 1989, Merritt 1978, Robbins et al. 1986b,

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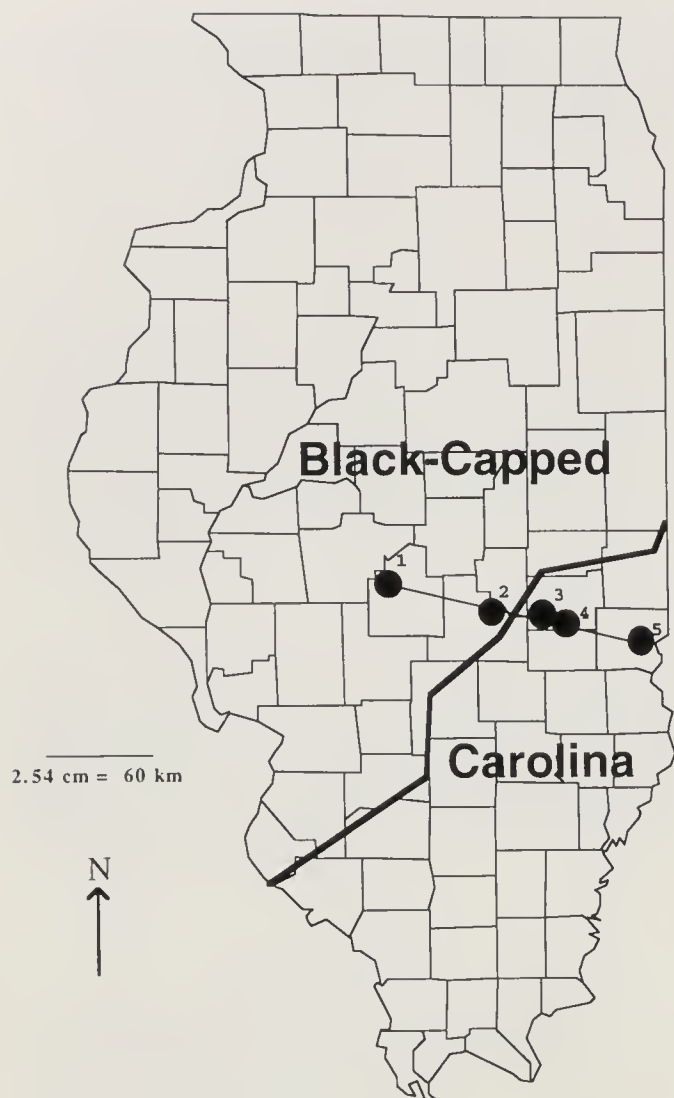


FIG. 1. Map of the study sites. Dark line indicates the historic contact zone across east-central Illinois (from Brewer, 1963). North of the contact zone represents Black-capped Chickadee range and south of the contact zone represents Carolina Chickadee range. Study sites are (1) Sangchris State Park, (2) Shelbyville State Park, (3) Douglas Hart Nature Center, (4) Fox Ridge State Park, and (5) Lincoln Trail State Park.

Ward and Ward 1974). The *chick-a-dee* call was used in this study because it contains sufficient information that can potentially be used by chickadees for individual recognition (Mamman and Nowicki 1981, Smith 1991). These calls tend to be short, less musical, less variable, and relatively specialized for particular functions such as alarm or changing the spacing between individuals (Smith 1991). The playback of *chick-a-dee* calls may elicit elevated calling rates (Nowicki 1983) by simulating intruding males (Hill and Lein 1989, Shackleton et al. 1992), and therefore would measure any differences in aggression levels between vocalization type.

Playback experiments were conducted 08:00–12:00 CST, 1 May–31 July 1995. Two different paired playback trials were conducted. One trial type consisted of broadcasting Black-capped and Carolina *chick-a-dee* call to chickadees in all study sites. The second trial

type consisted of playing both a randomly-selected chickadee call (Black-capped or Carolina) and a White-breasted Nuthatch vocalization. This second trial type was played every third trial at each study site. Nuthatches were used because chickadees should be familiar with this vocalization through winter flock association. Therefore, the responses to the nuthatch vocalizations gave us a baseline level of aggression to compare to the responses to chickadee vocalizations.

Playback trials were conducted by slowly walking around the study site until chickadees were detected. Trials were conducted by approaching a single bird as close as possible without visibly agitating it. Only data that fit the following criteria were used: (1) the focal bird could be approached within 15 m, and (2) weather conditions matched those required for the Breeding Bird Survey (Robbins et al. 1986a). Each bird was exposed to only one trial (either a two-chickadee trial or a chickadee-nuthatch trial), and specific areas within each study site were used for only one trial to avoid influencing neighboring chickadees. The minimum distance between trial locations was 500 m and was usually over 1000 m. Vocalizations were played for 2 minutes with a 5 minute silent period between the two sets of vocalizations. The silent period allowed the focal bird to return to normal activity after being exposed to the first vocalization. The order of the two vocalizations were alternated to reduce bias (Kroodsma 1989, Lampe and Baker 1994, Ward and Ward 1974).

Statistical analyses.—The degree of aggression by the focal bird was quantified based on its behavior during the two-minute trial period (Table 1). The identity of species at each study site was assumed to be that of historic record, although the possibility of hybridization may render this assumption invalid. However, all analyses were conducted without regard to species identity. Response scores were analyzed by paired *t*-tests. To compare all chickadee calls combined to nuthatch vocalizations, one trial per site was used and all sites were pooled together. The relationships between mean aggressive response and both date and distance to the contact zone were analyzed by Pearson Correlation Analysis (SAS Institute 1994).

RESULTS

Chickadees responded more aggressively to Black-capped and Carolina chickadee calls combined than to songs of White-breasted Nuthatches ($t = 4.6$, $df = 9$, $P < 0.001$; Fig. 2). Chickadees also responded more aggressively to each chickadee species call separately than to White-breasted Nuthatch vocalizations (Black-capped: $t = 8.9$, $df = 4$, $P < 0.001$; Carolina: $t = 5.65$, $df = 4$, $P < 0.005$; Fig. 2).

There was no significant difference in aggressive response to Carolina calls versus Black-capped chickadee calls ($t = 1.06$, $df = 33$, $P > 0.05$; Fig. 3). Chickadees within tra-

TABLE 1. Categories of behavioral responses for Black-capped Chickadees (*Poecile atricapillus*) and Carolina Chickadees (*Poecile carolinensis*) to playbacks of conspecific and heterospecific calls. Categories were derived by combining information from Brindley (1991), Censky and Ficken (1982), Ficken and Wiese (1984), Popp and coworkers (1990), Schroeder and Wiley (1983), and Shackleton and coworkers (1992). The categories run on a 0–10 scale with 10 being the most aggressive.

Category	Behavior
10	Flights <2 m from tape player, wing twittering
9	Flights 2–5 m from tape player
8	Flights <5 m from tape player, >2 gargles
7	Flights <5 m from tape player, <2 gargles
6	Flights 5–10 m from tape player, >4 calls made
5	Flights 5–10 m from tape player, <4 calls made
4	Flights 5–10 m from tape player, songs elicited
3	Flights >10 m from tape player, calls elicited, some gargling
2	Flights >10 m from tape player, songs elicited
1	minimal interest shown in recording, moving away from area
0	no interest, left area during trial

ditional Black-capped Chickadee range did not respond significantly more aggressively to Black-capped calls than to Carolina calls ($t = 1.35$, $df = 12$, $P > 0.05$; Fig. 3). However, chickadees within traditional Carolina Chickadee range were more aggressive towards Carolina calls than Black-capped calls ($t = 2.75$, $df = 20$, $P < 0.01$; Fig. 3).

When sites were analyzed separately, only chickadees at Fox Ridge State Park responded significantly more aggressively towards a given chickadee vocalization. Chickadees at Fox Ridge responded more aggressively to Carolina calls than Black-capped chickadee calls ($t = -2.74$, $df = 8$, $P < 0.03$; Fig. 3).

Aggressive responses towards both Black-capped ($r = -0.71$, $n = 5$) and Carolina chickadee vocalizations ($r = -0.29$, $n = 5$) increased at decreasing distances to the contact zone, although neither was statistically significant ($P > 0.05$). With both species combined, the relationship ($r = -0.49$, $P = 0.08$, $n = 10$) was still not significant ($P > 0.05$). Furthermore, chickadees did not show a sea-

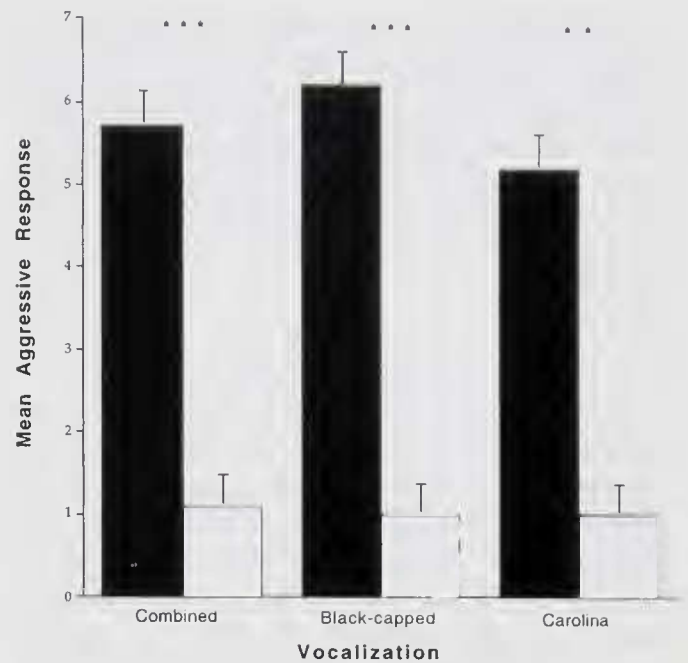


FIG. 2. Mean aggressive response of chickadees in paired Black-capped Chickadee-nuthatch ($n = 5$), Carolina Chickadee-nuthatch ($n = 5$), and for all trials combined ($n = 10$). Dark bars represent the response to chickadee calls and light bars represent the response to nuthatch vocalizations. ** $P < 0.01$, *** $P < 0.001$.

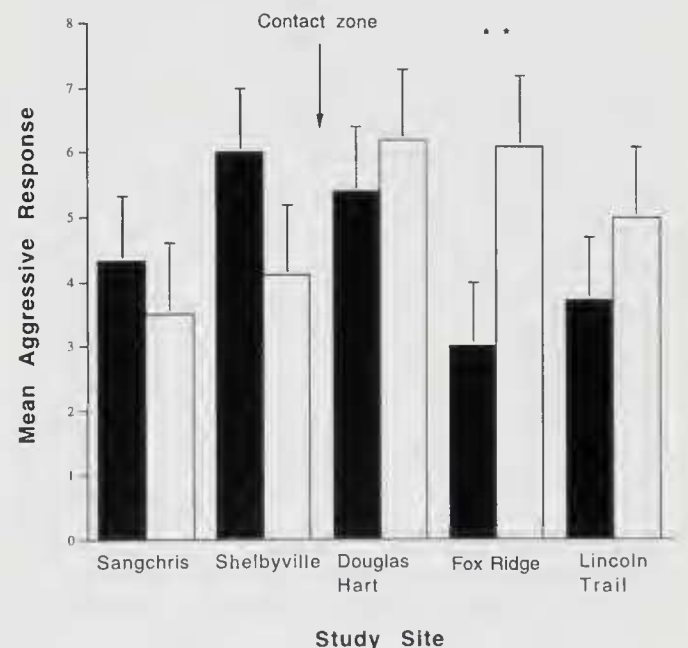


FIG. 3. Mean aggressive response of chickadees to Black-capped and Carolina chick-a-dee vocalizations at all study sites. Dark bars represent the response to Black-capped Chickadee calls and light bars represent the response to Carolina Chickadee calls. The study sites are arranged from West to East and the contact zone is noted between Shelbyville and Douglas Hart. (Sample sizes were 6, 7, 5, 9, 7 respectively; * $P < 0.05$.)

sonal difference in response, when all trials were combined ($r = -0.12$, $P > 0.05$, $n = 36$). Separately, there was no relationship between mean aggressive response to either Black-capped or Carolina Chickadee vocalizations and date ($r = -0.28$, $P > 0.05$, $n = 18$ and $r = 0.05$, $P > 0.05$, $n = 18$, respectively).

DISCUSSION

The fact that chickadees responded more aggressively to chickadee calls than nuthatch vocalizations indicated that chickadees were able to discriminate between congeneric and heterogeneric vocalizations (Fig. 2). These results are consistent with other studies that suggest that interspecific territoriality in chickadees is rare except with other chickadees in contact zones (Brewer 1963, Smith 1993).

We found that within the traditional Carolina Chickadee range, chickadees responded more aggressively to presumed conspecific calls. This is consistent with the results of studies on buntings in allopatric populations (Emlen et al. 1975) and in tropical birds in Peru (Robinson and Terborgh 1995). Several researchers found that chickadees responded more aggressively to their own song type than to songs of other chickadee species except in the contact zone where they responded aggressively to both conspecific and heterospecific song types (Ratcliffe and Weisman 1986, Robbins et al. 1986b). This differs from our results at one site. Chickadees at Fox Ridge State Park showed significantly more aggression to presumed conspecific vocalizations than towards heterospecifics. Overall, chickadees clearly responded more aggressively to chickadee calls than nuthatch calls with little difference between presumed hetero- and conspecific chickadee calls. This suggests that chickadees may either not perceive nuthatches as a competitive threat or that chickadees near contact zones may not distinguish between chickadee species calls.

We did not get the predicted increase in aggression towards heterospecifics closer to the contact zone. It is possible that the maximum distance from the contact zone used in this study was not far enough to detect any significant differences in aggression. This would suggest that chickadees across the area are familiar with congeners. Merritt (1981) sug-

gested that individual chickadees expand and contract their ranges seasonally. As the ranges of these species approach each other, cognizance of the heterospecific vocalization should increase (Ward and Ward 1974). At increasing distances from the contact zone, there could be a point where the mean aggressive responses would be significantly lower than closer to the contact zone.

Two other possible explanations exist for the aggression shown towards a presumed heterospecific call within species' ranges: misdirected aggression and the presence of hybrids. Misdirected aggression could arise from mistaken identity (Murray 1971, 1981). This is possible because the vocalizations of both species are similar and variable between individuals, and we used only one example of each vocalization type in this experiment (Mammen and Nowicki 1981, Smith 1991). However, this aggression could be intentional, because response to heterospecific calls may promote recognition and facilitate heterospecific spacing (Emlen et al. 1975, Merritt 1981, Robinson and Terborgh 1995). Hybridization may be more common in contact zones than previously thought (Brewer 1963, Johnston 1971, Rising 1968, Robbins et al. 1986b, Ward and Ward 1974). Thus, the lack of species specific aggressive responses could be the result of the presence of hybrids that are familiar with and respond similarly to calls of both species. If hybridization is the cause for the observed interspecific aggression, it is likely that interspecific territoriality may not act as a gap producing mechanism. Gaps between Black-capped and Carolina chickadee ranges may occur if hybrids within these gaps had severely reduced fitness (Brewer 1963). However, other factors may cause gaps. One such example is the lack of suitable habitat in gaps areas (Grubb et al. 1994).

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